Growth and morphology of rhizome cuttings and seedlings of salal (*Gaultheria shallon*): effects of four light intensities[1]

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Rhizome cuttings and seed of salal (*Gaultheria shallon*) were cultured in nursery beds at four light intensities (20, 50, and 70%, and full sunlight) created by various thicknesses of shade cloth. After each of two growing seasons, growth and morphological characteristics were compared among light intensities and between life stages. Under all light intensities, rhizome cuttings produced aerial stems and new rhizomes within 1 year and produced fruit within 2 years. Seedlings produced numerous aerial stems but few rhizomes. In general, 70% light induced the greatest production of aerial stems and rhizomes for both cuttings and seedlings. In 70% light, cuttings averaged more than three times the number of rhizomes and rhizome biomass and nearly twice the aerial stem biomass of cuttings in 20% light. Morphology of aerial stems, rhizomes, leaves, and seedling canopies was also affected by light quantity. Aerial stems produced by cuttings were shortest (9.9 cm) in full light and rhizome lengths were longer (27.6 cm) in 50% light than in 20% or full light. Specific leaf area of both cuttings and seedlings was highest (99.9 cm^2/g and 146 cm^2/g, respectively) under the most shaded treatment. The implications of these results with respect to the ecology of salal under field conditions are discussed.

Key words: *Gaultheria shallon*, seedlings, rhizome cuttings, shade treatment, morphology, vegetative growth.

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En utilisant différentes épaisseurs de tissus opaque, les auteurs ont cultivé en pépinière, des plants de *Gaultheria shallon* (salal) obtenus de boutures et de semences, sous quatre intensités lumineuses (20, 50 et 70% et pleine lumière). Après chacune de deux saisons de croissance, ils ont comparé la croissance et la morphologie obtenues sous les différentes intensités lumineuses et pour les différents stades du développement. Sous toutes les intensités lumineuses, les boutures de rhizome produisent des tiges aériennes et de nouveaux rhizomes en moins d'un an et des fruits en moins de 2 ans. Les plantules issues de semences produisent de nombreuses tiges aériennes mais peu de rhizomes. En général, 70% de lumière conduit à la production la plus importante de tiges aériennes et de rhizomes, que ce soit à partir des rhizomes ou de semences. Avec 70% de lumière, les boutures donnent en moyenne plus de trois fois le nombre de rhizomes, et la biomasse des rhizomes est presque deux fois plus grande que la biomasse des tiges aériennes, comparativement à 20% de lumière. La quantité de lumière affecte également la morphologie des tiges aériennes, des rhizomes, des feuilles et de la canopé. Les tiges aériennes produites par les boutures sont plus courtes (9,9 cm) en pleine lumière et les rhizomes sont plus longs (27,6 cm) avec 50% de lumière comparativement à 20% de lumière ou à la pleine lumière. La surface foliaire spécifique des boutures aussi bien que des semis est plus grande (99,9 cm^2/g et 146 cm^2/g, respectivement) sous les traitements les plus sombres. Les auteurs discutent la signification de ces résultats pour comprendre l'écologie du salal dans les conditions naturelles.

Mots clés : *Gaultheria shallon*, plantules, boutures de rhizomes, traitement par ombrage, morphologie, croissance végétative.

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Introduction

Salal (*Gaultheria shallon* Pursh.) is a common evergreen shrub of coastal forests from southern Alaska to central California. A rhizomatous species, salal relies on vegetative expansion to develop dense populations of ramets, which dominate forest understory plant communities (Long 1977; Messier and Kimmins 1991; Huffman et al. 1994) and compete with commercial tree species for moisture and nutrients (Black et al. 1980; Price et al. 1986; Vihnanek and Ballard 1988; Weetman et al. 1990). Salal responds vigorously above and below ground to mechanical disturbance and changes in environment. Within 8 years after clear-cutting forest overstories, salal ramet populations can reach more than 300 aerial stems/m^2, with belowground rhizome densities of more than 170 m/m^2 (Huffman 1993).

Field studies have shown that salal cover, productivity, and morphology are related to forest overstory density and canopy light transmission (Sabhasri 1961; Vales 1986; Bunnell 1990; Messier and Kimmins 1991; Smith 1991; Huffman et al. 1994). In addition to affecting light quantity in the understory environment, overstory density modifies light quality (Holmes and Smith 1977; Smith 1982), precipitation (Anderson et al. 1969; Azevedo and Morgan 1974; Harr 1982), and temperature (Kimmins 1987; Alaback and Tappeiner 1991). These factors, in turn, may determine levels of interference and symbiosis among forest plants.

Presently, few controlled experiments have been conducted to isolate the effects of light quantity on salal growth and morphology. Sabhasri (1961) found that shoot and root lengths and numbers of leaves of 1-year-old salal seedlings increased as growth-chamber light intensity varied from 100 to 400 foot candles (9.29 to 37.16 lx). Messier (1992) cultured salal cuttings in pots with conifer seedlings for two growing seasons under four shade and two nutrient treatments. He reported that salal biomass increased nearly sixfold as light increased from 5 to 100% full sunlight. Although light quantity affected leaf morphology, growing media nutrient status only slightly affected salal growth patterns.

Our study was designed to expand on Sabhasri's (1961) work and to examine effects of light in a more controlled way

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TABLE 1. Means (and SE) of salal rhizome and aerial shoot characteristics produced by cuttings after one growing season

Characteristic	Light intensity (relative light)			
	100%	70%	50%	20%
Rhizomes (no.)	3.8(0.66)*b*	5.2(0.55)*a*	3.5(0.44)*b*	1.7(0.30)*c*
Sum rhizome length (cm)	31.8(5.90)*b*	53.2(6.35)*a*	35.6(4.4)*b*	12.4(2.47)*c*
Individual rhizome length (cm)	8.3(0.57)*bc*	10.2(0.69)*a*	10.1(0.67)*ab*	7.1(0.69)*c*
Aerial stem (no.)	6.4(0.68)*ab*	7.9(0.73)*a*	5.8(0.41)*bc*	4.8(0.44)*c*
Aerial stem biomass (g)	2.1(0.32)*bc*	3.2(0.37)*a*	2.3(0.27)*b*	1.4(0.16)*c*
Aerial stem height (cm)	5.6(0.20)*c*	6.7(0.17)*b*	6.6(0.23)*b*	7.3(0.26)*a*

NOTE: The same letters, read across rows, denote statistically similar characteristic means at a significance level of 95%. Cuttings were harvested in April 1992.

than is possible in field studies. We cultured salal from both rhizome cuttings and seed and grew the plants for 2 years under four light intensities in outdoor nursery beds where rhizome development was relatively unrestricted. Our primary objectives were to determine the relative differences in salal productivity and morphology at different light intensities and to compare the characteristics of plants produced from rhizome cuttings with those developed from seedlings under these treatments.

Methods

Study environment

The 2-year study was conducted from 1990 to 1992 at the Forest Sciences Laboratory in Corvallis, Oreg. The climate of this area is typified by warm, dry summers and mild, wet winters. The average temperature in July is 21°C and in December it is 4°C. The annual precipitation is 107 cm/year (National Oceanic and Atmospheric Administration 1987).

Treatments

Four raised nursery beds, approximately 1.5 × 20 m in surface area, were filled prior to 1990 with local clay-loam soil. For our study, each bed was outfitted with a drip irrigation system. We used different thicknesses of commercially available neutral-filter shade cloth to create four light intensities. The light levels established, 20, 50, and 70% sunlight and full sunlight, were randomly assigned to quarters of each bed (beds were treated as replicates). The beds were irrigated evenly during the first growing season (1991) and hand-weeded at least once per week throughout the study period.

Rhizome collection

Rhizomes were collected in December 1990 from salal plants growing in the understory of a Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) stand located about 50 km west of Corvallis, Oreg. The stand was situated at approximately 270 m in elevation, and it had been commercially thinned about 8 years earlier. Young rhizomes, indicated by size (0.5 to 1.0 cm in diameter) and color, were selected and all aerial stems were removed. The rhizomes were cut into 30-cm segments, washed with tap water, and stored in a portable cooler.

Rhizome and seed planting

Within 6 h of collection, 40 rhizome cuttings were planted in each light intensity (40 cuttings × 4 light intensities × 4 beds). Spacing of cuttings within treatments was 10 cm and planting depth was 1–3 cm.

Salal seeds, collected and prepared as described by Huffman (1993), were also sown in the four nursery beds. One hundred seeds were sown in each of 10 circular plots per light intensity. Plots were 15 cm in diameter. As the seedlings grew, they were thinned, leaving the largest seedlings, to reduce the effects of intraspecific competition. At the beginning of the second growing season, all but two of the largest seedlings were removed per plot (20 per light intensity × 4 light intensities × 4 beds).

Rhizome measurements

After one growing season, 10 rhizome cuttings per treatment from each bed were randomly selected for excavation (160 total). Measurements of cuttings included number of new rhizomes, individual rhizome length, number of aerial stems, and height of individual aerial stems. Rhizomes and stems from cuttings were oven-dried at 70°C for 48 h and weighed to determine biomass.

In August 1992, after two growing seasons, a second sample of 160 cuttings was excavated from the beds and measured. At this time, the presence of fruit or flowers was also recorded for each cutting. To be classed as fruiting, at least one aerial stem for a cutting had to have produced flowers. Further, 20–25 leaves and 15–45 fruits were collected per treatment per bed. Mature leaves were randomly selected from all aboveground shoots; insect-damaged leaves were not sampled. One-sided leaf area was measured with an optical planimeter. Leaves and fruits were oven-dried at 70°C for 48 h and weighed. The number of seeds per fruit was counted after fruits were dried.

Seedling measurements

In August 1992, after two growing seasons, 10 seedlings from each light intensity (160 total) were randomly selected. The number of aerial stems, seedling height, canopy diameter, and number of rhizomes were measured. The aboveground and belowground (mainly roots) components of the seedlings were separated and oven-dried at 70°C for 48 h to determine biomass. Mature leaves were collected and leaf area and weight determined as described for cuttings.

Data analysis

One-way analyses of variance (ANOVA) were used to test for main effects due to light intensity ($p \leq 0.05$). When main effects were observed, least significant difference (LSD) tests were used to compare means of cutting and seedling characteristics for the four light intensities. Means were significantly different when p-values were less than 5%. All data were natural log or square root transformed when necessary to normalize distributions.

Results

Rhizome and aerial stem development from rhizome cuttings

First growing season

Cuttings in all light intensities produced rhizomes and aerial stems in one growing season. Sprouting was most common from buds at the distal and proximal ends of the cuttings. The greatest number of rhizomes produced by an individual cutting was 18 under 70% light, and the maximum total rhizome length was 160 cm (full light). The greatest length for an individual rhizome was 67 cm (70% light). As many as 26 aerial stems were found for a single cutting and 71% of all aerial stems were between 3 to 8 cm in height.

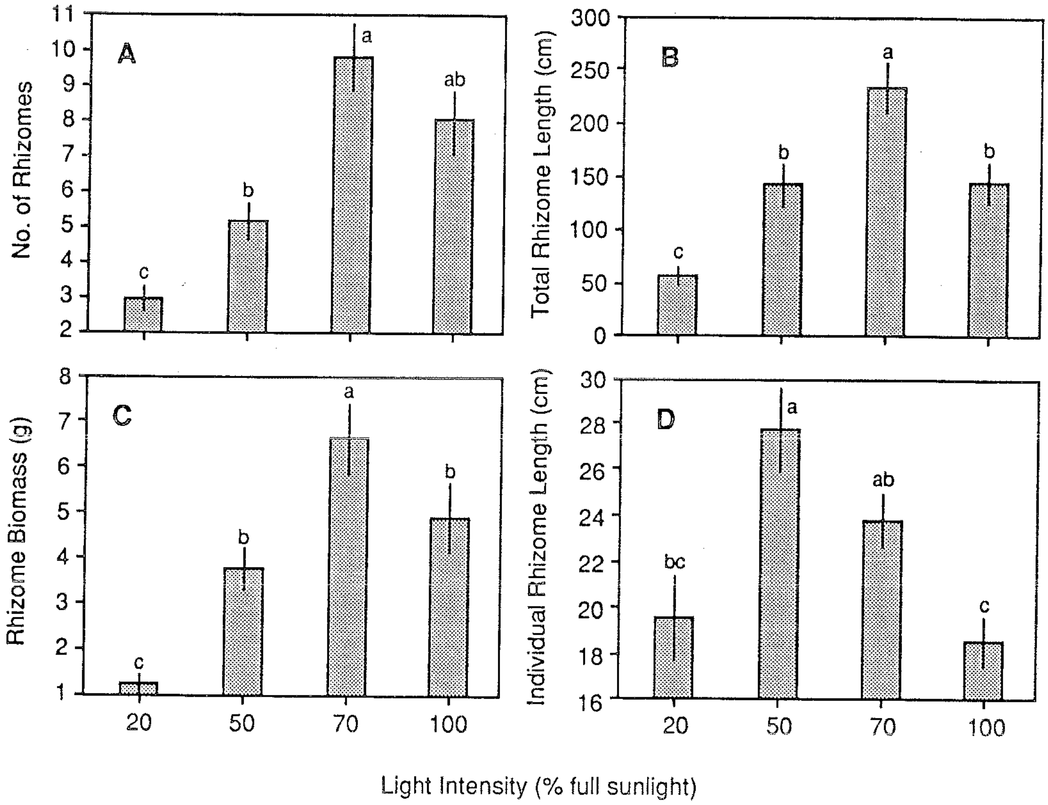

FIG. 1. Rhizome characteristics produced after two growing seasons by salal cuttings cultured under four light intensities. The same letters denote statistically similar means at a 95% significance level.

TABLE 2. Percent increase of salal rhizomes and aerial shoots produced by cuttings in four light levels

Characteristic	Light intensity (relative light) 100%	70%	50%	20%
Rhizomes (no.)	108	88	48	76
Sum rhizome length (cm)	355	338	299	367
Individual rhizome length (cm)	123	132	173	174
Rhizome biomass (g)	77	95	57	29
Aerial stems (no.)	130	72	74	81
Aerial stem biomass (g)	814	516	578	628
Aerial stem height (cm)	77	82	123	89

NOTE: Rates were calculated from treatment averages for harvest No. 1 in April 1992 and harvest No. 2 in August 1992.

Production and morphology of aerial stems and rhizomes were significantly different ($p \leq 0.05$) among light intensities (Table 1). In 70% light, cuttings produced the greatest number of rhizomes and had the greatest total rhizome length. More aerial stems with greater total biomass were produced in 70% light than in lower light intensities. However, the number of aerial stems in 70% light was not significantly greater than in full light. On average, rhizomes were shorter and aerial stems taller at 20% light than at higher light intensities. Rhizome biomass was not significantly different among light intensities. Rhizome biomass at this time included the biomass of the cuttings that produced during the growing season. The greater weight of the cuttings compared with the new rhizomes may have obscured any trends in these data.

Second growing season

Cuttings in 70% light were the most productive after two growing seasons (Fig. 1). At this light intensity, the maximum number of rhizomes produced by a cutting was 29, and the maximum total rhizome length was 592.0 cm. Cuttings in the 20% light intensity produced the fewest rhizomes with the lowest total rhizome length. Fifty-percent light and full light had statistically similar mean values for rhizome number and total rhizome length.

The length of individual rhizomes was greatest for cuttings in 50% light (Fig. 1). The longest rhizome of any cutting (154 cm), however, was produced under 70% light. Individual rhizome lengths in 20% light were statistically similar to those in 70% and full light. In full light, relatively short rhizomes were produced.

In 70% light, rhizome biomass was significantly greater than in other light intensities (Fig. 1). The lowest rhizome biomass was produced in 20% light. Specific rhizome weight (dry weight per cm of rhizome) was significantly greater in full light (0.036 g/cm) than in the 70, 50, and 20% light intensities (0.026 g/cm, 0.027 g/cm, and 0.021 g/cm, respectively).

More aerial stems were produced at high than at low light intensities (Fig. 2). Stems produced at 20 and 50% light, however, were significantly taller than those in 70% and full light. Stems produced by cuttings in full light were the shortest. Sum aerial stem biomass was not statistically different for cuttings in full, 70, and 50% light, but these were significantly greater than at 20% light (Fig. 2). In 20% light, there was a significantly smaller rhizome to aerial stem biomass ratio (0.14) than in full, 70, and 50% light (0.22, 0.32, and 0.25, respectively).

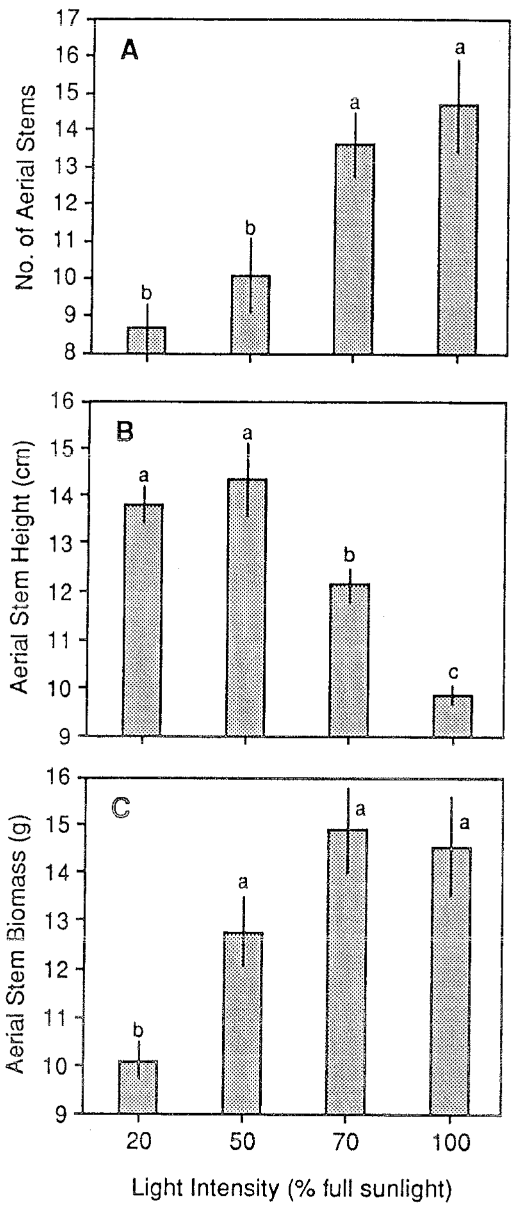

FIG. 2. Aerial stem characteristics produced after two growing seasons by salal cuttings cultured under four light intensities. The same letters denote statistically similar means at a 95% significance level.

Percent increase (PI) in numbers, lengths, and weights of rhizomes and aerial stems, calculated as

$$[1] \quad \mathrm{PI} = \left(\frac{\text{growth year 2} - \text{growth year 1}}{\text{growth year 1}}\right) \times 100$$

determined from treatment means, appeared to be affected by light intensity. Percent increase for numbers of rhizomes and aerial stems and for aerial stem biomass were greater in full light than in other light intensities (Table 2). Rhizome biomass increased most in 70% light, whereas greater increases in rhizome length and aerial stem height were found for cuttings in 50 and 20% light.

Surface area of individual leaves was significantly (p = 0.003) affected by light intensity (Table 3). Leaves in 20% light were significantly larger than those from 70% and full

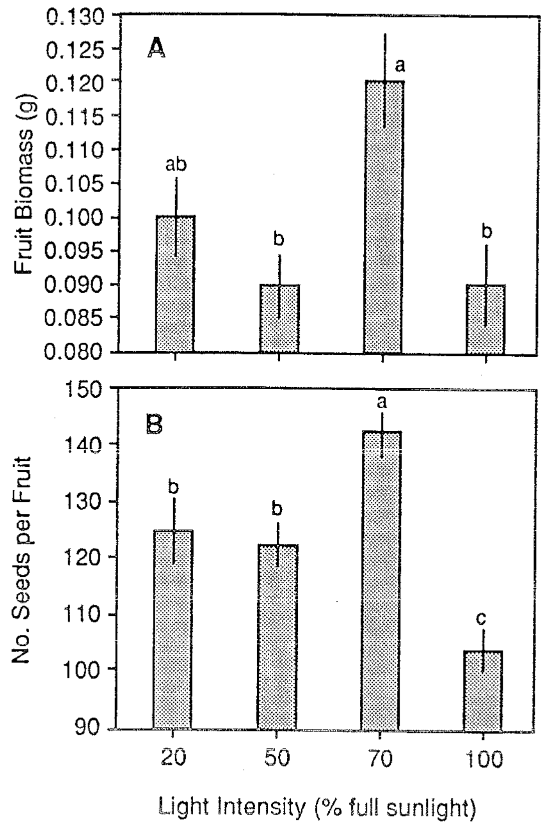

FIG. 3. Fruit characteristics produced after two growing seasons by salal cuttings cultured under four light intensities. The same letters denote statistically similar means at a 95% significance level.

light. Leaves in 50% light were larger than those in full light but not statistically different than leaves in 70 or 20% light. There was no statistical difference in mean leaf weight among light intensities. Specific leaf area (SLA = leaf area/leaf weight) was significantly ($p < 0.0001$) affected by light intensity (Table 3). Leaves produced in 20% light had the highest SLA. Values for leaves in 50% light were higher than those of 70% and full light, which were not significantly different from each other.

From 70 to 90% of all cuttings produced flowers and (or) fruit. Light significantly ($p = 0.001$) affected fruit dry weight (Fig. 3). Fruits produced in 70% light had significantly greater dry weight than those produced under full and 50% light, whereas fruits produced under 20% light were intermediate in dry weight. Light level also affected ($p < 0.0001$) number of seeds per fruit (Fig. 3).

Seedling characteristics

The percentage of seedlings with rhizomes varied from 7.5 to 25%, with the highest production at 70% light (Table 4). Considerably fewer seedlings produced rhizomes than did cuttings (93–100% of all cuttings produced rhizomes). The maximum number of rhizomes produced by any seedling was four (full light); the longest rhizome produced was 13 cm (50% light).

Significant ($p \leq 0.0002$) differences were found among light intensities for number of aerial stems, seedling height, seedling canopy diameter, and seedling biomass (Table 4). Seedlings in 70% light produced significantly more aerial

TABLE 3. Means (and SE) of leaf characteristics produced from salal cuttings in four light levels

Characteristic	Light intensity (relative light)			
	100%	70%	50%	20%
Leaf area (cm^2)	12.7(1.1)*c*	15.9(1.6)*bc*	17.9(1.1)*ab*	20.9(0.7)*a*
Leaf weight (g)	0.19(0.01)*a*	0.23(0.02)*a*	0.22(0.01)*a*	0.21(0.01)*a*
Specific leaf area (cm^2/g)	67.7(0.63)*c*	69.4(1.90)*c*	81.7(1.63)*b*	99.9(3.58)*a*

NOTE: The same letters read across rows denote statistically similar means at a 95% significance level.

TABLE 4. Means (and SE) of salal rhizome and aerial shoot characteristics produced by seedlings propagated in four light levels

Characteristic	Light intensity (relative light)			
	100%	70%	50%	20%
Aerial stems (no.)	10.9(0.76)*ab*	12.4(0.74)*a*	9.8(0.61)*b*	6.2(0.48)*c*
Seedling height (cm)	11.4(0.59)*c*	15.2(0.53)*b*	17.3(0.71)*a*	14.9(0.70)*b*
Seedling canopy diameter (cm)	11.4(0.65)*b*	14.0(0.46)*a*	13.7(0.44)*a*	11.5(0.49)*b*
Rhizome production (% of seedlings)	15.0	25.0	15.0	7.5
Aboveground biomass (g)	2.8(0.33)*b*	5.9(0.47)*a*	5.1(0.49)*a*	1.3(0.12)*c*
Belowground biomass (g)	0.51(0.06)*b*	0.74(0.05)*a*	0.50(0.06)*b*	0.17(0.01)*c*
Total seedling biomass (g)	3.3(0.38)*c*	6.7(0.50)*a*	5.6(0.53)*b*	1.5(0.14)*d*
Aboveground:belowground biomass ratio	5.9(0.48)*c*	8.8(0.67)*b*	12.1(0.85)*a*	8.0(0.47)*b*
Leaf area (cm^2)	5.8(1.08)*b*	8.0(0.94)*ab*	9.4(1.45)*a*	7.3(1.04)*ab*
Leaf weight (g)	0.069(0.012)*ab*	0.081(0.011)*ab*	0.086(0.013)*a*	0.052(0.008)*b*
Specific leaf area (cm^2/g)	83.5(0.54)*a*	99.6(2.69)*b*	108.9(5.37)*b*	146.0(4.24)*a*

NOTE: The same letters read across rows denote statistically similar characteristic means at a significance level of 95%.

stems than in 50 and 20% light but not more than seedlings in full light.

Aerial stem height in 50% light was significantly greater than in other light intensities; stems in full light were the shortest (Table 4). Mean canopy diameter in 70 and 50% light was significantly greater than in full light and 20% light.

The aboveground biomass of seedlings in 70 and 50% light was significantly greater than for those in full and 20% light (Table 4). Belowground biomass of seedlings was also greatest in 70% light. Total seedling biomass was greatest in 70% and lowest in 20% light (Table 4). Seedlings in 50% light produced significantly more total biomass than those in full light. Seedlings in 50% light had a significantly greater aboveground to belowground biomass ratio than seedlings in other light intensities; the smallest ratio was in full light (Table 4).

Leaf area in 50% light was greatest, but it was only significantly ($p \le 0.05$) greater than that in full light. Similarly, leaf weight was greatest in 50% light but was only significantly ($p \le 0.05$) greater than that in 20% light. Specific leaf area of leaves in 20% light was significantly greater than SLA of leaves in other light levels. In fact, SLA values in 20% light were nearly two times larger than those in full light and almost 1.5 times those in 70 and 50% light (Table 4).

Discussion

Vegetative reproduction

Most impressive is the ability of salal to resprout vigorously from rhizomes, especially in partial shade, producing networks of rhizomes and aerial stems, as well as fruit and seeds within 2 years. Interestingly, fruit production has been previously found only on stems greater than 5 years old and only under open overstory conditions (Bunnell 1990). Our results indicate that stem age may be less important to fruit production than are rhizome vigor and light environment.

In our study, total rhizome length increased by a factor of 10 over rhizome cutting length under 70% light intensity. Vigorous resprouting of salal has been reported in other studies (Sabhasri 1961; Messier and Kimmins 1991; Messier 1992; Huffman et al. 1994). For example, salal has been shown to account for up to 77% of the aboveground biomass on clear-cut and burned sites 2 years after disturbance on Vancouver Island, British Columbia (Messier and Kimmins 1991). In Oregon clearcuts 6 to 8 years old, Huffman et al. (1994) found salal populations with up to 177 m/m^2 total rhizome length. New rhizome production for these populations was about 6 m/(m^2-year). Other ericaceous shrubs such as *Calluna*, *Kalmia angustifolia*, and *Vaccinium* spp. similarly sprout from stem bases and rhizomes following disturbance (Minore et al. 1979; Calmes and Zasada 1982; Mallik and Gimingham 1983; Mallik 1993; Matlack et al. 1993).

The rapid reoccupation of aboveground and belowground space by salal can constrain or preclude regeneration of coniferous tree species, yet it can also be desirable on some sites. Dense patches of salal compete with tree seedlings for moisture (Black et al. 1980; Price et al. 1986) and nutrients (Weetman et al. 1990), immobilize nutrients (Messier and Kimmins 1990), and severely reduce light reaching the forest floor (Messier et al. 1989). However, these patches can also contribute to soil stability (Brown and Hafenrichter 1962), provide wildlife browse (van Dersal 1938; Cowan 1945), and are of economic importance, providing a "special forest product" used as floral greenery (Dimock et al. 1974). The latter use of salal is receiving increasing attention in Oregon.

Biomass

Even with adequate soil moisture, our results indicate that salal growth is somewhat inhibited in full light when compared with light shade (70% light). Similarly, Vales (1986) found high levels of light intensity had a negative effect on salal stem biomass under field conditions. Messier (1992) reported no significant difference in total biomass of salal between full and 30% light or between 5 and 10% light for salal cuttings grown in pots. Large differences were found, however, when the higher light levels were compared with the lower intensities. The response of salal to light intensities between 30% and full light was not examined in Messier's (1992) study. Further, we suggest that a restricted soil environment, such as that in a pot, may affect salal rhizome growth and thus affect total biomass. Additionally, competition with other persistent understory species, such as salmonberry, which also grows well in high light conditions (Tappeiner et al. 1991), will reduce salal growth in open environments.

Under field conditions, stands of Douglas-fir, a common overstory in salal's range, rarely transmit as much as 70% of the direct sunlight (Vales and Bunnell 1988). Therefore, comparisons of salal growth in field studies are generally made between full sunlight and much lower light levels (e.g., Vales 1986; Bunnell 1990; Huffman et al. 1994). This can lead to the apparently false conclusion that salal growth increases absolutely with increasing light intensity.

Morphology

Morphology of salal cuttings and seedlings was affected by differences in light intensity. For example, we found that seedling and vegetative stems in full light were consistently shorter than those at lower light intensities. Similarly, Vales (1986) found salal shoot size (height and diameter) to be adversely affected by high transmission of solar radiation through the overstory. We also found that individual rhizome lengths were relatively longer in 50 and 70% light and shorter in full and 20% light. Specific weight (g/cm) of rhizomes in partial shade was 58–75% of that in full light. Relatively higher specific rhizome weights in full light may be a response to drought stress as aboveground organs are exposed to higher temperatures and low relative humidity (J. Zaerr, personal communication). These differences in morphology plus variation in numbers of stems and rhizomes produced at different light intensities could produce different clone forms over time. In high light environments, clones would likely be compact with short rhizomes and stems. In contrast, clones in low light environments would likely be relatively sprawling with fewer, longer rhizomes and aerial stems. Light, nutrients, soil structure, and soil chemistry have all been found to affect clone compactness in other species (Lovett-Doust 1981; Salzman 1985; Slade and Hutchings 1987; Schmid and Bazzaz 1990). Plasticity in clone form may facilitate persistence of salal under varying light conditions. For example, a sprawling form with longer stems and rhizomes may help move ramets into sun flecks or out from under leaf canopies. Levels of resource integration among salal ramets are not known, but integration would likely enhance clone persistence in heterogeneous environments.

Leaf area and SLA values generally increased with decreasing light intensity. Smith (1991) reported SLA values of 50–80 g/cm^2 for salal sun leaves and 95–120 for shade leaves growing in forest conditions. Messier (1992) reported similar trends in leaf area for salal grown from cuttings at varying light intensities, although values for individual leaf area reported by Messier (1992) were smaller than those observed in this study. Similar variations in leaf morphology have been reported for other forest species (Tucker and Emmingham 1977; Fetcher et al. 1983; Goulet and Bellefleur 1986). Smaller, denser leaves may increase the photosynthetic efficiency of a plant in conditions of full sunlight or decrease transpiration rates in hot, dry environments (Nobel 1991).

Cuttings versus seedlings

Differences between salal rhizome cuttings and seedlings explain that rapid dominance of a site after disturbance is generally accomplished by resprouting from rhizomes rather than by seedling invasion. For example, seedlings produced relatively few rhizomes in over 2 years and these were only 8% the length of those produced by cuttings. Although both seedlings and cuttings produced similar numbers of stems over the 2-year study period, those of cuttings weighed from three to seven times more than those of seedlings. Leaves produced by cuttings were more than twice as large as seedling leaves.

Our results illustrate characteristics of salal seedlings that may make them more sensitive than clones to environmental conditions. For example, seedling SLA values were up to 140% greater than those of cuttings. Thus, seedlings may be more susceptible to drought stress than are clones. This is consistent with the findings of Huffman et al. (1994), who reported that salal seedling establishment was essentially restricted to rotten logs in partial shade with very low survival in clearcuts. Sabhasri (1961) found that freezing temperatures in May killed nearly all germinants. Further, seedlings apparently do not have the ability to expand vegetatively and produce ramets until they are more than 2 years old. Older plants, theoretically, can sample their environment and forage for resources by extending rhizomes for distances approaching 1 m/year (Huffman et al. 1994). Huffman et al. (1994) studied salal population dynamics for a range of overstory conditions and substrates. However, relatively little is known with respect to genet demography. Specific information regarding genet numbers, age distribution, and rates of genet mortality is needed to enhance our understanding of the natural history and ecology of salal.

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